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Phenology and survival of sporophytes in Dutch populations of *Buxbaumia aphylla*

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Two Dutch populations of *Buxbaumia aphylla* (Nunspeet and Elspeet) were studied for two generations (2014–2015 and 2015–2016). At both sites the number and developmental stages of sporophytes were frequently recorded and sporophyte maturity indices and survival rates were determined. The timing of sporophyte development was similar between the two generations but differed between the growth sites with earlier sporophyte development at Nunspeet. The growth sites are located close to each other and share the same climate and soil characteristics. The growth site at Nunspeet, however, is shaded and consequently a higher soil moisture early in the season might explain early sporophyte development. Sporophyte survival was extremely low, especially at Nunspeet (0.4% and 0.9% in 2014–2015 and 2015–2016 respectively) due to fungi and, possibly, slugs and birds.

In bryophytes, the study of phenology includes the timing of all aspects of growth and reproduction (Stark 2002a). General stages in the life cycle of bryophytes include spore germination, gametophyte formation, development of gametangia and sporophyte formation (Forman 1965, During 1979). Phenological studies in bryophytes may explore the complete life cycle of multiple bryophyte species (van der Wijk 1960) or may more specifically aim at a single species or a single life cycle event (Laaka-Lindberg 2005). It is well established that species differ largely between each other in life strategy and reproductive timing (van der Wijk 1960, During 1979, Miles et al. 1989) and that moss phenology depends on environmental factors such as temperature and precipitation (Busby et al. 1978, Zehr 1979, Furness and Grime 1982, Laaka-Lindberg 2005, Stewart and Mallik 2006). There are, however, only few bryophyte species for which the phenology within and between populations has been extensively studied.

Sporophyte populations of the bryophyte *Buxbaumia aphylla* Hedw. were subjected to some detailed studies on phenology and survival (Hancock and Brassard 1974, van Rompu and Stieperaere 2002). *Buxbaumia aphylla* is a remarkable species as it has disproportionate large sporophytes in comparison with its tiny gametophytes. Consequently, only the sporophytes reveal its presence in the field. In western Europe, *B. aphylla* is a rare species. In the Netherlands and Belgium it is known from only a few locations (van Rompu and Stieperaere 2002, van der Kolk 2014, De Beer 2014). The species grows on sandy soils, burnt places, coal bings and decaying wood (Steven and Long 1989, Sabovljević and Stevanović 2000, van der Kolk 2014). It prefers growing on algal crusts on disturbed sandy and somewhat humic soils, where it is accompanied by other mosses and lichens (e.g. *Cladonia* species) (van der Wijk 1956, Hancock and Brassard 1973, Smith 2004, van der Kolk 2014). Young sporophytes appear in autumn and become mature by April till June (Hancock and Brassard 1974, van Rompu and Stieperaere 2002). Populations of *B. aphylla* were previously studied by Hancock and Brassard (1974) in Canada and van Rompu and Stieperaere (2002) in Belgium. Here, I did observations on sporophytes on two populations of *B. aphylla* in the Netherlands over two generations. I tested whether phenological timing differed between the locations and between both seasons. I compared the results with previous phenological studies on the species.

Methods

Site descriptions

I observed sporophyte development and survival in Dutch populations of *Buxbaumia aphylla* at Nunspeet and Elspeet. Both populations were initially found in the winter of 2013–2014 and are located at graveyards on the Veluwe in the province of Gelderland (van der Kolk 2014). The growth

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site at Nunspeet is located 11 km northwards of the growth site at Elspeet.

Nunspeet

The population is located on the eastern graveyard in Nunspeet (52°22′51.6″N, 5°79′70.7″E). *Buxbaumia aphylla* grows within an area of 1.2 × 0.8 m on humic sandy soil in between two stone graves (Fig. 1a). A large beech tree *Fagus sylvatica* L. is located directly south of the growth site, sheltering the growth site and preventing direct sunlight reaching the soil surface. The growth site is largely covered with bryophytes and lichens, while there are only few vascular plants present. Dominant bryophyte species are *Polytrichum piliferum* Hedw., *Hypnum cupressiforme* Hedw. and *Cephaloziella divaricata* (Sm.) Schiffn. Furthermore, *B. aphylla* is accompanied by terrestrial lichen species, including *Peltigera didactyla* (With.) J.R. Laundon, *Peltigera rufescens* Hook. F. and several *Cladonia* species.

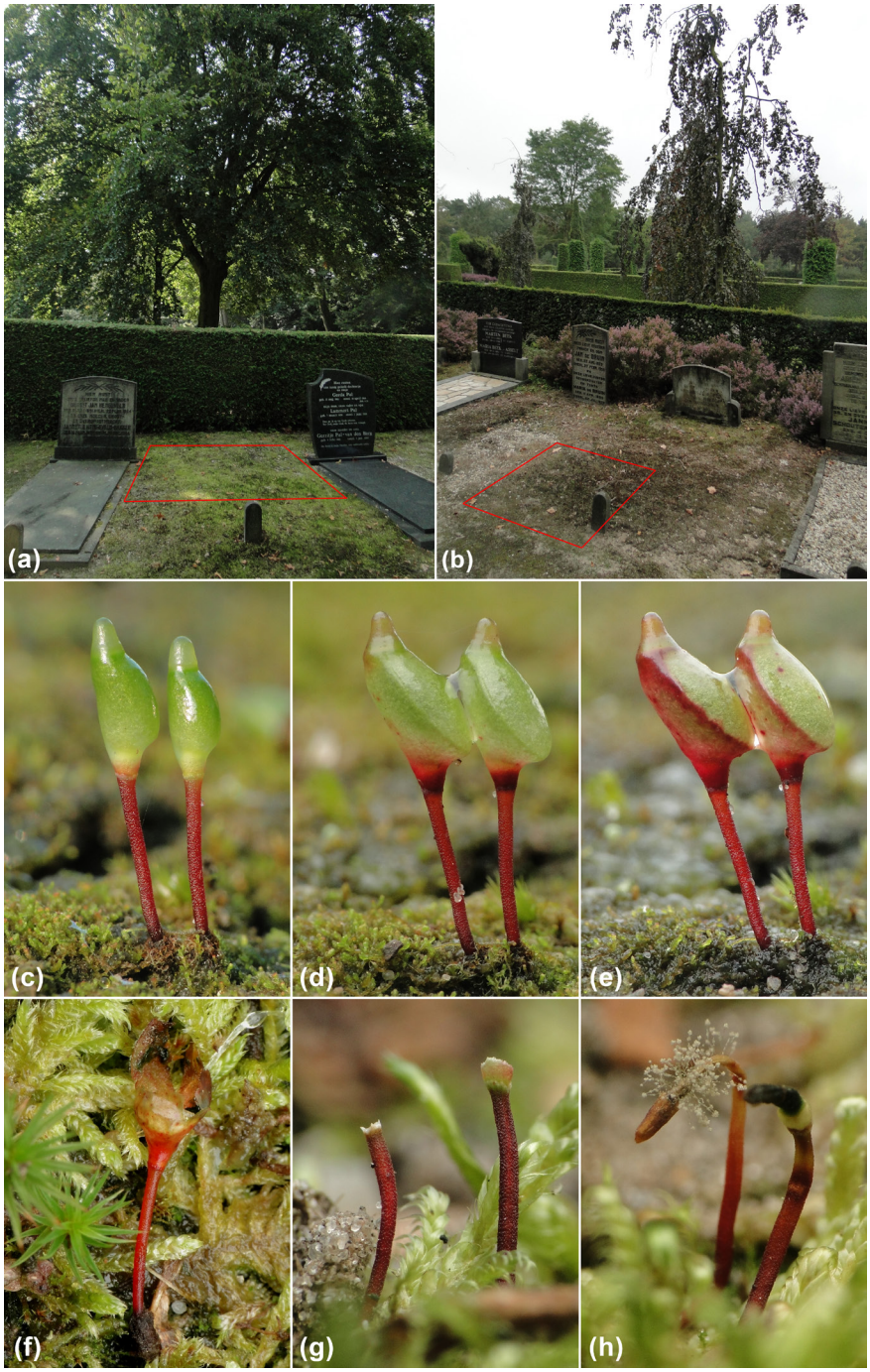


Figure 1. Dutch populations of *Buxbaumia aphylla*. (a) Growth site at Nunspeet in southward direction; (b) growth site at Elspeet in southward direction; (c–e) *B. aphylla* sporophytes on 1 November 2014 (sporophyte stages 7 (right) and 8 (left)), 20 November 2014 (stage 9) and 11 December 2014 (stage 10) at Elspeet, respectively; (f) pulled out sporophyte (20 November 2014, Nunspeet); (g) sporophytes with eaten capsules (20 September 2014, Nunspeet); (h) sporophytes infected by parasitic fungi (20 September 2014, Nunspeet).

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Elspeet

The second population of *Buxbaumia aphylla* is located at the graveyard of Elspeet, located immediately south of the village (52°17′7.0″N, 5°47′8.8″E). At this locality, *B. aphylla* grows on an area of 0.8 × 0.8 m on humic sandy soil in front of a gravestone (Fig. 1b). Except from a small recently planted beech tree *Fagus sylvatica* south of the growth site the locality is highly exposed. Similarly as at the growth site at Nunspeet, the growth site at Elspeet is largely covered with bryophytes and lichens, including the species *Polytrichum piliferum*, *Hypnum cupressiforme* and *Cephaloziella divaricata* that are also found at Nunspeet. Additionally, the invasive moss species *Campylopus introflexus* (Hedw.) Brid. is present at Elspeet. The lichen species accompanying *B. aphylla* at Elspeet include *Peltigera rufescens* and several *Cladonia* species.

Sporophyte recordings

Both populations of *B. aphylla* were regularly visited between September 2014 and May 2016 to monitor the number and development of the sporophytes. This period covers two sporophyte generations: 2014–2015 and 2015–2016. The populations at Nunspeet and Elspeet were both visited on the same days. However, the population at Elspeet was not structurally monitored between January and July 2015, because a significant proportion of sporophytes was damaged or had disappeared due to human activities in December 2014. For the 2014–2015 generation, I visited Nunspeet 18 times and Elspeet 12 times between September and July. For the 2015–2016 generation, I visited both locations 15 times between August and May. There were no significant cold spells during the study period.

During every visit, I thoroughly investigated a fixed plot (Fig. 1a–b) within the growth site, thereby counting the number of sporophytes within those plots and recording their developmental stages. 12 developmental stages can be distinguished in the sporophyte development of *B. aphylla*, where stage 1 represents the youngest stage (calyptra visible on soil surface) and stage 12 represents mature spore-releasing capsules. The developmental stages of *B. aphylla* were described in detail by Hancock and Brassard (1974). The developmental stages differ from each other by the length and colour of the seta and the shape, colour and size of the capsule (examples of different stages in Fig. 1c–e). I did not record stage 1 sporophytes as they are hardly recognizable in the field due to their tiny appearance. Thus, only 11 stages were recorded during this study, corresponding to stages 2–12 described by Hancock and Brassard (1974). I recorded the number of damaged sporophytes during the early visits in the season. The setae of damaged sporophytes often remain visible for a long time in the field. Consequently, they are a useful indicator of the total number of developed sporophytes (van Rompu and Stieperaere 2002).

Data analysis

For every visit and for both populations a sporophyte maturity index (SMI), representing the average sporophyte developmental stage, was calculated, using a formula introduced in previous phenological studies on bryophytes (Longton and Greene 1967, Solli et al. 1998):

$$I = \frac{\sum_{i=1}^{s} M_i r_i}{r_{\text{tot}}}$$

in which I is the sporophyte maturity index, M_i the rank number of developmental stage i, s the total number of developmental stages (12 for *Buxbaumia aphylla* sporophytes), r_i the number of sporophytes in stage i and r_{tot} the total number of recorded sporophytes.

I used linear regression with SMI as response variable to determine whether sporophyte development differed significantly between the locations and between seasons. I included only those counts in the model for which 2 > SMI > 9. The development of the populations within this range of the SMI approximated a linear trend. Day in the season (Day 1 is 1 August), Season (2014–2015 and 2015–2016) and Location (Nunspeet and Elspeet) were included in the regression model. The model was fitted using the *glm* function in R (<www.r-project.org>).

Additional to the phenological analysis, I calculated the total minimum number of sporophytes that had developed during the current generation for every visit for both localities, based on the total number of living sporophytes and the number of setae without capsules. Based on the total number of developed sporophytes and the number of healthy sporophytes, I calculated survival rates for every visit.

Results

Table 1 presents the number of recorded capsules, the total number of developed sporophytes, the sporophyte maturity index and the capsule survival of the studied populations of *Buxbaumia aphylla* for all site visits. For the 2014–2015 generation, a total of 235 sporophytes developed at Nunspeet and 47 at Elspeet. For the 2015–2016 generation, a total of 113 sporophytes developed at Nunspeet and 12 at Elspeet.

Developmental phenology

The phenological patterns that I observed were similar between the seasons, but differed significantly between the two populations (Fig. 2, Table 2). On 8 September 2014, sporophytes were already present at Nunspeet, while sporophytes appeared between 6 October 2014 and 18 October 2014 at Elspeet. In 2015, sporophytes had appeared at Nunspeet between 3 September and 17 September, while at Elspeet sporophytes appeared between 8 October and 17 October. Thus, sporophyte development started about one month later at Elspeet compared to Nunspeet in both seasons. Growth speed was similar at both sites. Most sporophytes were full grown (stage 9) by the first half of November at Nunspeet and by the first half of December at Elspeet. Unfortunately, due to extremely high sporophyte mortality, I could not reliably study the timing of ripening and spore release of the sporophytes. At Nunspeet, the only remaining capsule in the 2014–2015 generation started releasing spores between 16 May and 24 June. At Elspeet, at

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Table 1. Number of living capsules, total number of developed sporophytes, sporophyte maturity index and capsule survival for the 2014–2015 and 2015–2016 generations for populations of *Buxbaumia aphylla* at Nunspeet and Elspeet. The growth site at Elspeet was highly damaged on 22 December 2014 and therefore not intensively monitored between January and July 2015.

	Nunspeet				Elspeet			
	Capsules	Developed sporophytes	Sporophyte maturity index	Capsule survival (%)	Capsules	Developed sporophytes	Sporophyte maturity index	Capsule survival (%)
2014–2015								
8-Sep-14	145	146	2.5	99.3	0	0	0.0	–
13-Sep-14	202	223	3.1	90.6	0	0	0.0	–
20-Sep-14	156	223	3.5	70.0	0	0	0.0	–
27-Sep-14	79	235	4.5	33.6	0	0	0.0	–
6-Oct-14	32	235	6.1	13.6	0	0	0.0	–
18-Oct-14	19	235	6.9	8.1	14	14	3.1	100
1-Nov-14	18	235	8.3	7.7	31	35	5.7	88.6
11-Nov-14	16	235	8.9	6.8	39	45	6.8	86.7
20-Nov-14	13	235	9.2	5.5	39	45	8.1	86.7
4-Dec-14	12	235	9.8	5.1	40	47	8.7	85.1
11-Dec-14	12	235	9.8	5.1	40	47	8.9	85.1
22-Dec-14	10	235	9.9	4.3	–*	–	–	–
23-Jan-15	8	235	10.0	3.4	–	–	–	–
7-Mar-15	5	235	10.0	2.1	–	–	–	–
16-Apr-15	3	235	10.0	1.3	–	–	–	–
16-May-15	1	235	11.0	0.4	≥5	47	12.0	≥10.6
24-Jun-15	1	235	12.0	0.4	–	–	–	–
30-Jul-15	1	235	12.0	0.4	–	–	–	–
2015–2016								
27-Aug-15	0	0	0.0	–	0	0	0.0	–
3-Sep-15	0	0	0.0	–	0	0	0.0	–
17-Sep-15	37	37	2.3	100	0	0	0.0	–
26-Sep-15	56	58	3.5	96.6	0	0	0.0	–
8-Oct-15	87	105	5.5	82.9	0	0	0.0	–
17-Oct-15	92	113	6.9	81.4	2	2	2.0	100
31-Oct-15	80	113	8.4	70.8	12	12	4.8	100
7-Nov-15	72	113	9.0	63.7	8	12	6.3	66.7
21-Nov-15	49	113	9.7	43.4	8	12	8.1	66.7
4-Dec-15	39	113	9.8	34.5	7	12	9.0	58.3
18-Dec-15	35	113	9.9	31.0	4	12	9.5	33.3
8-Jan-16	32	113	10.0	28.3	3	12	9.3	25.0
27-Feb-16	22	113	10.0	19.5	0	12	–	0.0
16-Apr-16	5	113	10.0	4.4	0	12	–	0.0
14-May-16	1	113	11.0	0.9	0	12	–	0.0

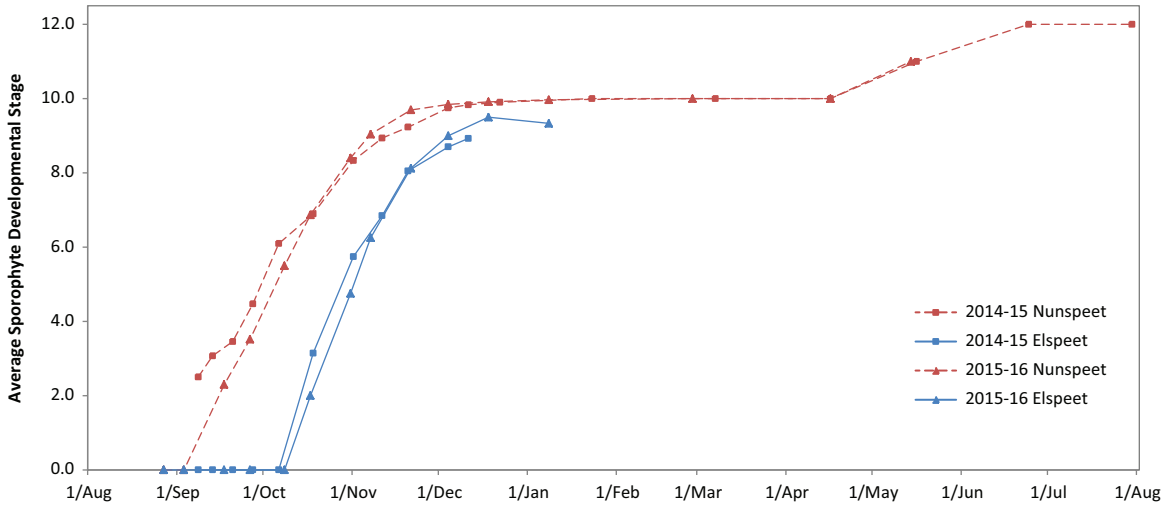


Figure 2. Sporophyte maturity index for populations of *Buxbaumia aphylla* at Nunspeet (shaded growth site) and Elspeet (exposed growth site) for the 2014–2015 and 2015–2016 generations. The number of sporophytes differ for every data point and are provided in Table 1.

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Table 2. Linear regression model results for the effect of day, location and season on sporophyte maturity index. Significant p-values are highlighted.

	Estimate	SE	t-value	p
Day in season	0.116	0.007	17.042	**< 0.0001**
Location (Nunspeet)	3.244	0.350	9.273	**< 0.0001**
Season (2015–16)	–0.297	0.260	–1.142	0.268

least five sporophytes survived the growth site destruction in December 2014 and they released spores at 16 May 2015.

The sporophytes at Nunspeet appeared about 10 days later in 2015–2016 compared to 2014–2015. Overall, however, the phenological patterns were in 2015–2016 highly similar to the phenological patterns in 2014–2015 for both growth sites (Fig. 2).

Sporophyte survival

Sporophyte survival was extremely low for the 2014–2015 generation at Nunspeet (Table 1). At Nunspeet, sporophytes were pulled out, capsules were eaten and sporophytes were infected with parasitic fungi (Fig. 1f–h). Eventually, only 1 out of 235 sporophytes survived over the whole season. Most sporophytes died during young developmental stages in September and October. In 2014–2015, sporophyte survival was much higher at Elspeet, where 85.1% (40 out of 47) sporophytes survived until 11 December. This is considerably higher compared to the sporophyte survival at Nunspeet where survival was 6.8% (16 out of 235) on 11 November with a similar sporophyte maturity index of 8.9. For the 2015–2016 generation, survival at Nunspeet halfway the season was higher compared to the 2014–2015 generation: 34.5% (39 out of 113) of the sporophytes survived until 4 December (5.1% (12 out of 235) survival on 4 December 2014 for 2014–2015 generation). In both generations, the maturity index for the visits on 4 December equalled 9.8. At Elspeet, none of the 12 developed sporophytes survived by 27 February 2016.

Discussion

The growth sites of *Buxbaumia aphylla* at Nunspeet and Elspeet are very similar, yet the sporophytes developed one month earlier at Nunspeet in both the 2014–2015 and 2015–2016 generation. Considering the wide distribution range of *B. aphylla* the study sites are located very close to each other (10.7 km) and resemble each other in climate conditions, soil type and vegetation. For example, at both sites *B. aphylla* is accompanied by *Polytrichum piliferum*, *Cephaloziella divaricata*, *Cladonia* and *Peltigera*. However, differences in light exposure between the localities might have caused the observed difference in timing of sporophyte formation. The locality at Nunspeet is sheltered by a large beech tree, which avoids sunlight to reach the growth site of *B. aphylla*. In contrast, the locality at Elspeet is highly exposed, enabling high evaporation even in autumn and winter. Supportively, I observed that the soil was moist throughout the whole season at Nunspeet, while the surface soil layer at Elspeet was often dry in August, September and October. It would require simultaneous soil moisture measurements at both growth sites during multiple seasons to confirm these observations. Nevertheless it is well established that moisture and humidity are important environmental factors influence bryophyte growth and timing. Evaporation stress might limit moss growth, as has been observed in the moss species *Tomenthypnum nitens* (Hedw.) Loeske (Busby et al. 1978). Also, rainfall has been demonstrated to influence timing and speed of development in desert mosses (Stark 2002b) and in the boreal bryophyte *Lophozia silvicola* Buch (Laaka-Lindberg 2005). In the closely related *Buxbaumia viridis* (DC) Moug. & Nestl., moisture and precipitation are important for spore germination and establishment (Wiklund 2002, Wiklund and Rydin 2004). In Australia, two nearby populations of *Dicranoloma platycaulon* Dixon where also shown to differ in their phenological timing, but this difference was more likely due to frost being more severe at one of the localities (Milne 2001). I further observed that timing of *B. aphylla* sporophyte formation was fairly similar between the generations. However, over longer time periods the timing might as well vary between generations. van der Valk (2011), for example, showed that the timing and duration of phenological stages in *Brachythecium rutabulum* (Hedw.) Schimp. highly varied between years.

The timing of sporophyte formation at Nunspeet is comparable to previous studies in Belgium and Canada, where sporophytes were first observed in September (Hancock and Brassard 1974, van Rompu and Stieperaere 2002). Both in the 2014–2015 generation as in the 2015–2016 generation, most sporophytes at Nunspeet reached developmental stage 10 in December. Hancock and Brassard (1974), however, observed that 54.8% of the sporophytes had reached developmental stage 10 by 30 April in a Canadian population of *Buxbaumia aphylla* in the 1972–1973 generation. This large difference might be due to frost and snowfall in the winter of 1972–1973 at the Canadian locality in comparison with the mild Dutch winters of 2014–2015 and 2015–2016. I cannot exclude that a different interpretation of developmental stages 9 and 10 between me and Hancock and Brassard (1974) might partly account for the observed difference as well. The difference between developmental stages 9 and 10 cannot be observed by a clear distinguishable morphological feature, but involves a gradual change in colour and size (Hancock and Brassard 1974). Mature sporophytes were observed in May (Elspeet) and June (Nunspeet), but the number of sporophytes was too low to conclude on differences between the Dutch populations and previous studies. Consequently, I cannot conclude whether timing of sporophyte production early in the season affects the timing of spore release in spring.

Survival was very low for the sporophyte generations of 2014–2015 and 2015–2016 at Nunspeet as only one out of 253 and one out of 113 sporophytes matured, respectively. The total number of developed sporophytes in 2014–2015 may actually be more than 253, as I did not track individual sporophytes and therefore could not account for capsules that completely disappeared in between visits. Especially at Nunspeet, I observed that sporophytes were pulled out, that capsules were eaten and that some sporophytes were affected by parasitic fungi. Birds (e.g. *Turdus* species which are abundant at Nunspeet) were probably responsible for pulling out

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sporophytes, whereas slugs could have eaten the capsules of the sporophyte where only the stalk remained. Future studies could make use of cameras to record herbivore presence at the field sites and confirm the mortality causes. Interestingly, sporophyte mortality was much lower at Elspeet for the 2014–2015 generation. As the growth site of Elspeet is more exposed and drier, it might be a less attractive foraging site for birds and slugs. For the 2015–2016 generation, sporophyte mortality was higher at Elspeet. However, only a few sporophytes had developed at Elspeet. Low survival rates of sporophytes, 29% in 1971–2072 (41 out of 144 sporophytes) and 13% in 1972–1973 (8 out of 61), were previously observed in populations of *B. aphylla* in Newfoundland in Canada (Hancock and Brassard 1974). In a Belgium population of *B. aphylla*, survival rates of 8.4% in 1998–1999 (8 out of 95), 12.5% (1 out of 8) and 6.0% (3 out of 50) were reported by van Rompu and Stieperaere (2002). Hancock and Brassard (1974) found that heavy frost resulted in a high sporophyte mortality, whereas van Rompu and Stieperaere (2002) mention birds and slugs as possible predators. Based on the current studies it is likely that often very few sporophytes mature in populations of *B. aphylla*. However, as millions of spores are produced in one capsule (Kreulen 1972), even a few mature sporophytes might guarantee the dispersal of spores to uncolonized sites.

Concluding remarks

Buxbaumia aphylla is a species in which the sporophytes develop through 12 distinguishable phases. Especially early in the season, valuable data on timing of development can easily be recorded by visiting multiple populations on the same day. Here, I showed how two Dutch populations differ in timing of sporophyte development although their growth sites resemble each other. Future studies on the phenology of *B. aphylla* might link differences in timing between populations and seasons to environmental variables (e.g. soil moisture) and examine if timing of sporophyte development in spring affects the timing of spore release in spring.

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